

Variability in space and time and redundancy as stabilizing principles of forest humus profiles

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Abstract

Forest humus profiles exhibit high stability against deposition of acids. Their morphology has not substantially changed during the period between about 1960 and 1985. This means that the overall activity of the saprophagous soil animal communities has not changed either. Explanations for this stability are to be found at the abiotic level as well as at the autecological and the synecological level of the animals. This paper focusses on the stabilizing principle of redundancy, scarcely considered up until now, which is understood as the ability of species to substitute for each other in ecological functions. This principle seems to play an important part in humus biocoenoses. For all of the four functions of soil animals determining humus profile morphology, viz. comminution of plant residues, coarse mixing of organic and mineral material, fine mixing of these and fabric formation, there are examples for redundancy. In the functions comminution and fine mixing the possibilities of replacement of an eliminated species by others probably are much more manifold than in coarse mixing and fabric formation. These functions are exerted mainly by earthworms which are replaceable only by a few species, most of them being other earthworm species.

Keywords: Saprophagous soil animals, Litter transformation, Humus profiles, Stability, Redundancy, Spatial variability, Soil acidification.

Hétérogénéité spatio-temporelle et redondance comme facteurs de stabilité du profil des humus forestiers.

Résumé

Les profils d'humus forestiers montrent une très forte stabilité à l'encontre des dépôts acides. Leur morphologie ne s'est pas substantiellement altérée durant la période 1960-1985; on en déduit que l'activité des peuplements d'animaux saprophages n'a pas changé non plus. Les causes de cette stabilité sont d'ordre abiotique, autécologique et synécologique. La redondance, concept rarement utilisé, est présenté ici comme un principe de stabilité et interprétée comme la possibilité pour une espèce de se substituer à une autre avec la même fonction écologique. Ce principe joue apparemment un rôle important dans la formation des humus. Pour chacune des quatre fonctions écologiques assurées par les animaux du sol et qui donnent une empreinte à la morphologie des humus, à savoir le broyage des litières, le mélange des éléments organiques et minéraux grossiers, le mélange des éléments organiques et minéraux de petites tailles et la formation de la structure, il y a des exemples de redondance. Les possibilités pour une substitution des espèces dans les fonctions broyage des litières et mélange des éléments de petites tailles sont vraisemblablement plus diverses que dans les fonctions de mélange des éléments organiques et minéraux grossiers et de formation de la structure. Ces dernières fonctions sont assurées par des vers de terre qui sont remplaçables seulement par un petit nombre d'espèces dont la plupart sont d'autres espèces de vers de terre.

Mots-clés : Animaux saprophages, Transformation des litières, Profils d'humus, Stabilité, Redondance, Hétérogénéité spatiale, Acidification des sols.

INTRODUCTION

Decreases in soil pH have been found repeatedly in Central Europe since about 1955 (reviewed in Belotti, 1989, p. 4). This means that the life conditions of the litter transforming soil animals have deteriorated. The actual pH-values are below the optimum for many of these animals.

Soil animals exert a determining influence upon the morphology of humus profiles, *i.e.* the humus cover and the humus-rich mineral top-soil, by dominating the processes of litter comminution and mixing plant-residues with the mineral soil (Zachariae, 1965; Babel, 1975). These processes, therefore, were expected to have been slowed down and this retardation should become visible in humus profile morphology by increasing thickness and density of humus cover horizons. This, however, was not observed. In the following, we attempt to explain the stability of these morphologically recognizable processes.

In our investigations we reexamined the humus profiles of 38 forest sites (22 with conifers, 16 with beech or oak) in the Federal Republic of Germany after 10 to 25 years. The second examination was conducted in the same month as the first one in order to exclude seasonal fluctuations of humus profile features. The proton load the sites had received in this time by acid deposition was estimated by proton load or emission data of the region published by other authors, type of tree stand and duration of the influence (time between first and second investigation). The obtained values covered a range between 0.4 and 3 kmol H⁺ per ha and year and between 4 and 75 kmol H⁺ per ha over the investigation period.

We judged to be significant changes only those deviations in humus profile properties that exceeded the deviations found in investigations repeated in three consecutive years which were due to spatial variability, oscillations from year to year and deviations of estimation of the morphological humus features in the field. Sites with changes in vegetation by windthrow or severe thinning were excluded from the investigations as well as sites with tree stands younger than 50 years at the first investigation because in these cases changes in humus profile due to normal development of density of tree canopy had to be expected (Belotti, 1989).

Table I gives a survey over the results. Here the sites are grouped according to the estimated proton load they received over the investigation period. In most cases (27 out of 38) no clear changes were found, in 7 cases a slowing down, and in 4 cases an acceleration of the morphologically visible processes of litter transformation was found. There was no change into another humus form class. So there were, as before, 16 sites with the humus form class mull, 13 sites with a transition form between mull and mor or mor with a thin H-horizon and 9 sites with mor with a thick H-horizon.

Table I. – Changes in litter transformation velocity during the last 10 to 25 years in forests of the Federal Republic of Germany indicated by thickness and density of humus cover horizons in relation to estimated proton load.

Number of sites with litter transformation	Proton load over the investigation period (kmol H ⁺ per hectare)		
	< 15	20-30	40-75
– unchanged	23	1	3
– accelerated	1	0	3
– slowed down	4	2	1

The sites with alterations in humus profile features indicating a slowing down of litter transformation were not the sites that received the largest proton load.

A remarkable feature is the stability of mull, a humus form which conventionally is considered to be restricted to sites where anecic earthworms are abundant. It persisted even on those few sites which had a bulk pH lower than 4.0 at the end of the investigation period. (Old pH values in most cases of table I are not known.) In laboratory experiments *Lumbricus terrestris* Linnaeus, 1758 retreated from such acid areas, *Aporrectodea longa* (Savigny, 1826) even from soil with pH<4.5 (Laverack, 1961). Mechanisms which may enable earthworms to cope with such conditions in nature are discussed in section "Acid tolerance".

STABILIZING MECHANISMS

There are three groups of stabilizing mechanisms in ecological systems. They act at three hierarchic levels.

1. Physical and chemical buffering mechanisms concern the level of the abiotic life conditions.

2. Tolerance of organism species is challenged, if possibilities of buffering are surpassed so that the abiotic conditions change; this is the autecological level.

3. Redundancy of species as multiple occupation of ecological functions (Bormann, 1987) becomes relevant if single species are eliminated because their range of tolerance is surpassed. This kind of buffering is acting at the synecological level.

We assume that, especially, redundancy can explain our results on stability of forest humus profiles against acid deposition. This is presented in the following. We are aware of the fact that this mechanism has a limited capacity because, as acidification progresses, the range of more acid-tolerant species will be surpassed also. When an influence is so severe that the character of vegetation changes, *e.g.* when trees die and are replaced by other plant species, redundancy will fail to stabilize the humus profile. In this case a completely different decomposer community develops which will produce another type of humus profile. Such changes in decomposer community were found by Dunger

(1991) after the replacement of spruce trees by maple shrub due to fly-ash immissions. However, it appears to us from our own investigations and from literature that forest humus profiles are stabilized to an important part by redundancy in their processes as they are highly diversified in organism species and abiotic conditions in terms of space and time.

Acid-buffering

Ulrich (1981) differentiates buffer ranges in soils and names them after the buffering reaction dominating at the respective pH (determined in soil solution). The buffer ranges are those of carbonates (pH 8.6-6.2), primary silicates (6.2-5.0), cation exchangers (5.0-4.2), aluminium oxides (4.2-3.8), aluminium and iron oxides (3.8-3.0) and iron oxides (3.0-2.4). They are further characterized by different buffering capacities (protons per amount of buffering substance) and different buffering rates (protons per time unit). As a consequence, the buffer ranges are of different stability. Organic matter also acts as an acid-buffering agent, because of its content of Ca, Mg and K. *and, however, by its amino acid content*

From a comparison of the buffering rate in the silicate buffering range, i.e. the rate of proton consumption by weathering of primary silicates (0.2-2 kmol H⁺/ha *a) with the sum of internal proton production and deposition of protons and ammonium, Bredemeyer *et al.* (1990) concluded that all non-carbonaceous forest soils in Central Europe will pass or already have passed into the aluminium buffer range under present atmospheric deposition conditions.

Acid tolerance

For the development of humus profiles the adaptability of earthworms to increasing acidity is of particular importance. High acid tolerance is shown by the species *Lumbricus rubellus* Hoffmeister, 1843 which is widespread in forests of Central Europe. Nordström and Rundgren (1974) found *L. rubellus* occurring at pH (H₂O) 3.3 in the same abundances as at pH 6.6 in Southern Sweden, and termed the species pH-indifferent. *Lumbricus terrestris* occurred at pH values down to 3.5, but only in very low abundances at a pH lower than 4.5. Baltzer (1956) found in forests in northwestern Germany *Lumbricus rubellus* to be the only earthworm species in the humus cover of a podsol under pine with a pH (KCl) of 2.4, though occurring in very low abundance. In 5 out of 6 soils with a pH (KCl) between 2.8 and 3.2 the same species was found, in two of these soils *Aporrectodea caliginosa* (Savigny, 1826), in one of them *Dendrobaena octaedra* (Savigny, 1826).

In laboratory experiments where artificial soil was acidified to a pH (KCl) of 3.6 *Aporrectodea caliginosa* and *Lumbricus terrestris* produced more and larger

epidermal gland cells than in untreated soils. This probably resulted in an increased mucus discharge (Greven, 1987; Greven *et al.*, 1987). According to Lamparski (1985) the pH of the mucus of *Lumbricus badensis* (Michaelsen), 1907 is 6.0. Earthworms are able to increase soil pH in their vicinity by excreting NH₃ (Lee, 1985, pp. 213 ff.) or accumulating bases in their casts (Lee, 1985, pp. 224 f.). It can be assumed, therefore, that earthworms in soils whose mean pH is lower than the values tolerated by the animals are able in many cases to avoid acidosis by means of metabolic accommodation.

Redundancy

According to Bormann (1987) redundancy will be understood here as multiple occupation of functions in an ecosystem: "At the community level, redundancy is based on having more than one species of plant, animal or microbe capable of carrying out the same process ... One or several species may substitute for an impaired species and assume most of its functions".

Because of the importance we accord to redundancy, it will be treated in a section of its own. Prior to this, the fundamental functions of the soil animals for the processes evolved in humus profiles have to be demonstrated.

THE FUNCTIONS OF SOIL ANIMALS FOR THE MORPHOLOGY OF HUMUS PROFILES

Principally, four important functions of soil animals can be specified for the morphology of humus profiles, i.e. the humus cover and the humus-rich top-soil.

The comminution of plant residues (dead plant organs) results largely from the activity of animal primary and secondary decomposers (fig. 1). This comminution increases the surface area of dead plant tissue and so facilitates access of abiotic agents and microorganisms. It is especially efficient as it takes place repeatedly, although the terms tertiary, quarternary or even quintary decomposers are not common. Repeated comminution also means repeated translocation in a very small space, e.g. from the interior of an aggregate to the surface of another one which entails also a change in the conditions for decomposition.

A coarse mixing of plant residues (which may be entire organs or comminuted to a low degree only) with mineral soil material is exerted mainly by epigeic and anecic earthworms (fig. 2). Their main activity takes place in the few centimetres near the surface of the mineral soil. Here we are concerned with the pulling of dead leaves into the mineral soil by *Lumbricus terrestris* as well as the casting of mainly mineral material on or into the humus cover which is often observed to be done by *L. rubellus*. In a broad



Figure 1. – Communion of leaf residues, also of bud scales and root residues. Most of the picture is excrement material of larvae of Diptera (primary decomposers), particle size 100-200 μm . The bundle of three leaves top right has been left behind by the animals. Somewhat left and downwards from the centre a longitudinal section of a channel (width 300 μm) directed downwards with loosely packed droppings (around 50 μm) of enchytraeid worms (secondary decomposers). – Beech forest, F-horizon, mull-like moder, Terra fusca (chromic cambisol), jurassic limestone. – Thin section, natural height 3.4 mm.

sense, the mixing of portions of mineral soil which differ in humus content carried out by these two and other species, can also be mentioned here. Coarse mixing of organic and mineral material above all results in a better balance of the milieu of temperature and humidity for decomposition.

Fine mixing of organic particles (cells or small groups of cells which originate from organ comminution) with mineral material has to be separated from coarse mixing (fig. 3). It takes place at a microscopic scale and is the result of the ingestion of mineral soil together with organic material often or always carried out by representatives from all important groups of saprophagous soil animals—the only exception being the Oribatei. In the gut, a mixture of pieces with a size of a few μm s comes about which facilitates the chemical reaction of organic material with sesquioxides, clay minerals and other minerals.



Figure 2. – Coarse mixing. Bright aggregates of mineral material have been brought up by *Lumbricus rubellus* into the dark humus cover (H-horizon). Decomposed needle residues are mixed into the mineral material (immediately below centre). At the top the L-horizon with bright needles. – Spruce forest, L-, (F-), and H-horizon, moder, rendzina, Jurassic dolomitic limestone. – Polished soil block, natural height 28 mm.

Biological formation of aggregates and voids, i.e. fabric formation in the narrower sense, mainly results from the feeding of soil animals (fig. 4). The excrements often are aggregates with a characteristic form and then are termed droppings or fecal pellets. They often are deposited in groups and then inter-aggregate pores are formed. Well visible channels, which remain open for some time or are soon filled partly or completely, are formed almost exclusively by earthworms and enchytraeids. (The much larger burrows of soil-dwelling mammals and the breeding channels and cavities of insects can be ignored here because they are only exceptional in forest humus profiles. However, the activity of voles has to be dealt with, in section "Possibilities of replacement"). By this process, the number of coarse pores (>10 μm diameter) are influenced. They mainly determine the budget of air and poorly bound soil water. In addition, they are paths for roots, microorganisms and animals.

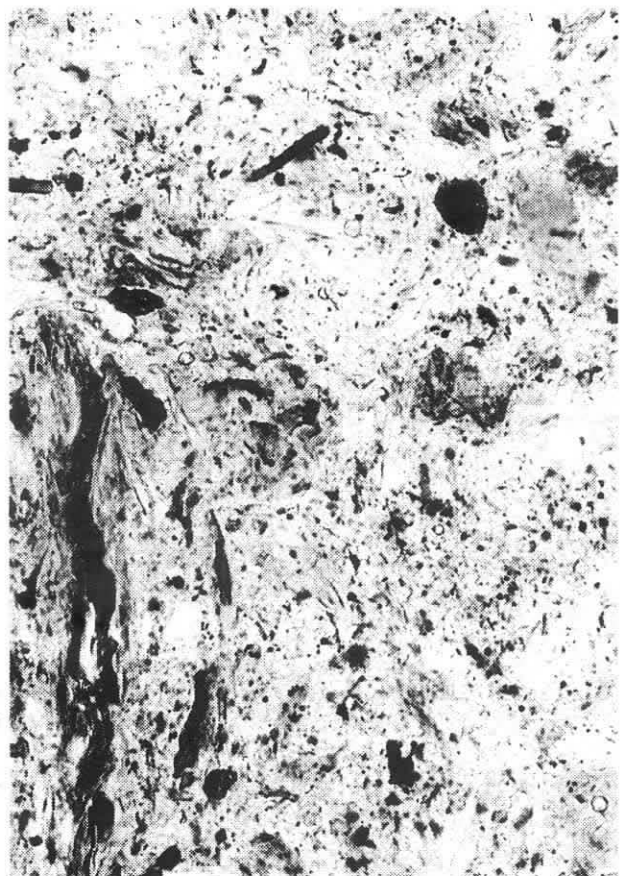


Figure 3. – Fine mixing. A tissue residue and varying cell residues are embedded in a dense, bright, nearly colorless matrix. The only well recognizable mineral grain is a prolate, 20 μm long quartz, running fairly parallel below a fungal hypha (top centre). From mid left to bottom left a residue of a tissue, probably a parenchymatic one. Numerous single cell residues which are often deformed are cut along their narrow or their broad side (these are all particles which are somewhat or much darker than the matrix). Most probably all the punctual, nearly black particles are organic, too. – Clear cut area after spruce with grasses, Ah horizon (detail from an earthworm cast), mull, Pseudogley (stagnic gleysol), triassic claystone. – Thin section, natural height 0.35 mm.

In these four groups of functions, which exert a decisive influence on the morphology of forest humus profiles, soil animals are far more significant than abiotic processes (*fig. 5*). By comminution, the litter is transformed from the state of the L-horizon* to the states of the F-horizon and the H-horizon. The last two horizons, however, do not develop if coarse mixing is carried out quickly enough. The H-horizon characterizes the mor (German Moder and Rohhumus, French moder or dysmoder), its absence characterizes the mull. By coarse mixing an Ah-horizon, in particular often a more humus-rich upper part, the Ahh-horizon (Babel, 1971), develops. Fine

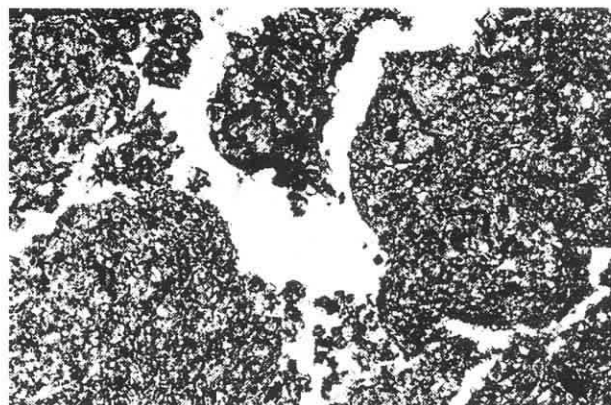


Figure 4. – Formation of aggregates and voids. The large dense zones on the right, top centre and on the bottom left are remains of earthworm casts (recognizable by the lobate contours), the one top centre is dark by high content of tissue residues. The inter-aggregate pore between is, in the lower part, loosely infilled with small aggregates (droppings of Enchytraeidae or Collembola). – Mixed deciduous forest, Ah-horizon, mull, Pseudogley (stagnic gleysol), loess. – Thin section, natural height 2.2 mm.

mixing influences the elementary fabric (Kubiena, 1938) of the Ah-horizon. Formation of aggregates and voids in the humus cover horizons F and H as well as in the Ah-horizon is a most important process in the development of the macrofabric of these horizons.

THE CONCEPT OF REDUNDANCY IN THE ZOOLOGY OF HUMUS PROFILES

A certain species diversity increases the probability, at least statistically, of species existing which are capable of substituting for each other in functions important for the stability of the ecosystem or, in our context, the humus profile. This probability is one reason for the widespread, but not generally true idea that species-rich systems should be more stable (Pianka, 1983, p. 316 f.; Kikkawa, 1986).

Humus profiles indeed are species-rich. This fact has given rise to Anderson's (1975 a) paper on "the enigma of soil animal species diversity". In this article he explains species diversity mainly by niche differentiation and temporal change.

Actually, the diversity in the morphology of humus profiles leads to the conclusion that they offer a multitude of possibilities of niche formation for saprophagous animals (*figs. 1-6*). This can be easily deduced from soil thin sections, for the niche parameters space and food, especially.

A specialization to narrow niches, however, does not take place for many species, because it is not required. Conditions change too fast and too unsystematically to

* In Germany, the symbols L, Of, Oh, where O stands for the humus cover, have been used for some years instead of the classical terms L, F, and H for the horizons of the humus cover.

allow species to develop abundances which would lead to competition and, consequently, to an equilibrium between species (Anderson and Healey, 1972). In other words, food is not the limiting resource in animal decomposer communities. Attempts to verify this hypothesis by manipulating litter input on experimental plots in temperate deciduous forests, however, led to conflicting results (David *et al.*, 1991; Schäfer, 1991). This may be partly due to the fact that litter manipulation induces changes not only in food supply but also in microclimate, thus having site-dependent negative or positive effects. Again and again, the animals are disturbed by abiotic conditions, especially extremes of humidity and temperature. These act as "rarefying agents" (Pianka, 1983, p. 313) which prevent competition, thus allowing high species diversity to be maintained. Rarefaction, according to this author, is the continual density-independent removal of organisms from a community. Besides extremes of abiotic conditions, predators are considered to be rarefying agents. Some studies indicate that predation pressure on saprophagous forest soil animal communities may be considerable (reviewed in Schäfer, 1991). Reduction of predator pressure was followed by increases in abundances of animal decomposers (Clarke and Grant, 1968) or their consumption rates (Lee, 1974). These findings suggest that predation pressure was another limiting factor. However, the influence of predation pressure on species diversity of animal decomposer communities in forests was not investigated. In marine ecosystems, however, the removal of a predator caused the extinction of individual prey species (Paine, 1966).

In this way, many species may exist together in changing dominance relations without being strictly specialized. Their activities may also strongly resemble one another. Respectively, different species may ingest, and thereby comminute, the same kind of plant residues or mix plant residues into the mineral soil and there produce similar kinds of soil fabric by similar kinds of activity. So redundancy in the sense of ability of mutual substitution, according to Bormann (1987), is explained quasi by itself. If one species is impaired for a shorter or longer period, it does not matter, other species will act in the same manner anyway.

The high degree of horizontal heterogeneity of forest humus profiles (*table II*, *fig. 5*) allows for the withdrawal of animals during unfavourable times to species-specifically more favourable places. Besides, there are also life strategies enabling animals to survive under hostile conditions while staying in place, e. g. diapause, cyclomorphosis, anhydrobiosis and others. For those species which need refuges, it is important that humus profiles strongly vary not only over distances of μm and mm , but also of cm and dm (Belotti, 1989).

The greater the distances to places with favourable conditions the more strongly, of course, is the population reduced during unfavourable conditions

Table II. – Range of respective properties of humus profiles on 5.4 m $\times$ 5.4 m large areas in a spruce stand and a beech-oak stand in southwestern Germany (Belotti, 1989). The minimal distances between the samples are 15 cm in parts of the areas, 60 cm in others.

Property	Spruce (n=192)	Beech-oak (n=202)
Thickness of the L-horizon (mm)	5-38	
Thickness of the F-horizon (mm)	0-25	
Thickness of the H-horizon (mm)	0-33	
Thickness of the HAh-horizon (mm)	0-44	
Number of leaf layers		0-35
Coherence of mineral soil ^{1,2}	3-5	1.5-5
Fine root density in mineral soil ^{1,2}	0-4	0-4
Value (Munsell) of the colour of mineral ^{1,3}	2-5	2-5
pH (CaCl ₂) of mineral soil ¹	3.14-4.09	3.44-4.29

¹ In the uppermost part of the Ah-horizon, 0-2 cm.

² Estimate values: 0: lacking; 1: very low, found after short searching; 2: found without searching, but not abundant; 3: medium, contributing to the aspect, but less than 25% of the volume; 4: high, 25 to 50% of the volume; 5: very high, more 50% of the volume.

³ Value after Munsell Soil Color Chart, on these sites mainly determined by humus content.

and the more time recolonization takes. In this context, it is important that in both forest stands in *table II* which are managed according to current practice the spatial variability of the humus profiles does not increase when distance between the profiles increases from 15 to 180 cm (Belotti, 1989).

The small-scale spatial mosaic of humus profiles is a mosaic of habitats for litter decomposers with different requirements upon their environment. The high degree of habitat diversity is in many cases undoubtedly the reason for the well-known high small-scale spatial variability of abundances of soil animals. However, it also creates the possibility of coexistence of species with the same food but different requirements upon the other environmental conditions in a small area and, thereby, widens the ecological valence of the community of all litter comminuting species in the area. Besides, it increases the probability that animals find refuge at unfavourable times. In the context of stability of humus profiles against soil acidification, the small-scale spatial variability of the pH is of particular interest. Microlocations with a higher pH could serve as refuges for acid-intolerant soil animals, such as anecic and endogeic earthworms during weather-induced peaks of acidification. The pH-ranges in *table II* exceed the critical values for many species. The sites in *table II* are typical for many forest soils in Germany.

There are further investigations in the literature on the questions of variability in time and space of humus profiles as well as of food identity, or degree of specialization of soil animals. More general concepts are those of the "fugitive" and the "opportunistic" species.

"Fugitive species", with their high dispersal ability, find new or abandoned habitats to the same degree as they are expelled from old ones by competition

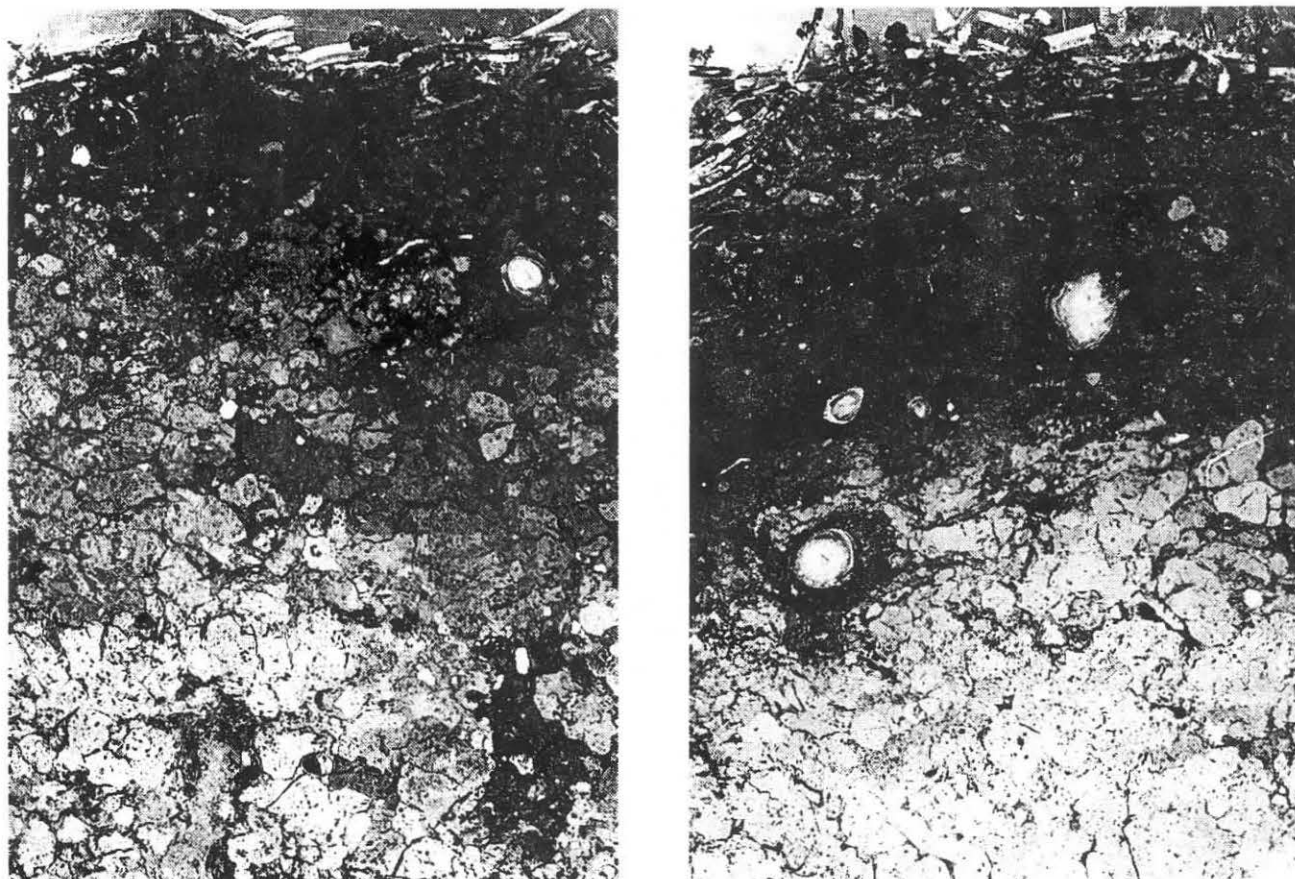


Figure 5. – Variability of humus profiles. Distance 15 m, same day of sampling, no essential difference in tree canopy, vegetation of the floor and relief. Left: 5 mm L-, 5 mm F-, 15 mm H-horizon, overlying an Ah-horizon with low humus content. Right: 3-5 mm L-, 0-3 mm F-horizon overlying a very dark Ahh-horizon (about 8 mm in top centre, appearing nearly black in the photograph) and an Ah-horizon varying in color by mixing activity of earthworms (*Lumbricus rubellus* and others). – Spruce forest, left side moder, right side mull, Terra fusca (chromic cambisol), Jurassic limestone. – Polished soil blocks, natural height 60 mm.

(Hutchinson, 1951). This strategy requires patchiness of the system which is given in forest humus profiles. From the litter comminuting soil animals the oribatid mite *Eupelops torulosus* C. L. Koch, 1840 (Hågvar and Kjøndal, 1981*) and, of course, the larvae of Diptera with their highly mobile adults may be considered to be fugitive species. Of the tipulids, the adults of *Tipula fulvipennis* Degeer, 1766 are characterized by an especially high motility even under very dry conditions (Freeman, 1968). Such species, according to Hågvar and Kjøndal (1981), may “temporarily or permanently take over important functions” when the ecosystem is disturbed by “unpredictable factors”. Fugitive species, however, are doubtless important in the normal annual course in forest humus profiles as well as, e. g., for the initial colonization of the litter after each litter fall.

The “opportunistic species” with their low degree of specialization and their ability to withstand extreme conditions may use commonly claimed resources at

places and in times where more competitive specialists are eliminated by extremes of weather or other conditions (Slobodkin and Sanders, 1969).

Temporal separation to an unknown degree contributes to avoidance of competition for food (Anderson, 1977). Collembola (Anderson and Healey, 1972) as well as oribatid mites (Harding and Stuttard, 1974) do not consume any food at all during long periods. Some oribatid species were observed to switch in autumn from litter diet to microorganism diet (Anderson, 1975 b). The two dominant macrophytophagous oribatid species in a Danish beech forest had their maximum feeding activity at different times of the year (Luxton, 1981). Weather conditions changing from year to year may promote different collembolan species (Joosse, 1969). The annual litter fall gives rise to microclimatic changes in the humus profile, which are modified by wind redistribution of the litter cover.

* The authors used the older name *E. duplex* sensu Berlese

Spatial separation of different species with nearly identical food was found in a laboratory experiment with two oribatid species of which one species in the presence of the other retreated from the F- into the L-horizon (Anderson, 1978). Similar results were obtained in investigations on two locally co-occurring oribatid species in nature (Siepel, 1990). This means that the two species are able to coexist, but when one of them is eliminated the other one will assume her functions.

The high variability of humus profiles in time and space corresponds to a high variability in diets which is a further reason for a high number of co-occurring species. It is true that colonization of the litter by microorganisms strongly influences its ingestion by soil animals (Hartenstein, 1962; Kühnelt, 1963; Latter, 1977; Cooke and Luxton, 1980; Ponge, 1991). A given species, however, may ingest a broad spectrum of litter types (Dunger, 1958; Pande and Berthet, 1973) and spectra of coexisting species show a high degree of overlap. An example is given in table III, taken from Pande and Berthet (1973). In this context, where we are concerned with the question if species are able to replace each other in the comminution of dominant litter types, it is decisive that the animals ingest the litter no matter if their real diet is the litter itself or the microorganisms growing on it. (It seems probable, however, that the observed palatability of a broad spectrum of litter types for "macrophytophagous" animals is mediated by colonization with microorganisms where preferences of animal species may differ much more. So by elimination of microorganism species, e. g. due to acid deposition, some litter types might become unpalatable for certain animal species and degree of overlap of palatable litter types might diminish.)

The broad spectra of diets allow the animals to shift to some other than the preferred diet in the presence of competing species. Anderson (1978) terms this phenomenon a "contraction of ... niches away from areas of overlap". When, on the other hand, a competing species is eliminated e.g. by acid precipitation, an expansion of the niche of the remaining species may occur which then assume that species function.

Table III. – Feeding preferences for three oribatid mite species from the humus cover in a stand of *Pinus nigra* (from Pande et Berthet, 1973)

Species	Feeding frequencies on		
	needles	twigs	bark
<i>Microtritia minima</i>	xxx	x	x
<i>Rhyssotritia duplicata</i>	x	x	xx
<i>Phthiracarus</i> sp.	x	xxx	0

High, medium, low, and very low frequencies of occurrence are designed with xxx, xx, x and 0.

POSSIBILITIES OF REPLACEMENT OF SOIL ANIMAL SPECIES IN THE PROCESSES OF HUMUS PROFILE FORMATION

As stated above, populations of saprophagous soil animals show a high diversity of species. The species tolerate changes in life conditions to different degrees. Their niches overlap in the food dimension. Substitution ability of species, at least to some extent, follows from all these observations. This means that stabilization of humus profiles by redundancy is possible. Some direct observations about substitution in the humus profile functions, mainly deduced from morphological investigations on the processes, are quoted here.

Substitution in the *comminution of plant residues* not only means comminution of the same residues but also comminution of residues in the same way. For example, this is the case when different oribatid species mine in needles of the same conifer species. Babel and Vogel (1989) concluded to substitution processes between enchytraeids and Collembola in the humus cover of a spruce stand. They had found that in spite of strong changes in the relative abundances of both groups of animals in a fertilization experiment, there was no alteration in the amount of droppings with maximum diameters from 60 to 130 µm, composed of organic fine substance, plant residues and a small portion of mineral grains, in the humus profile. Older examples which may indicate substitution for each other between different soil animal groups in the comminution of plant residues were presented by Zachariae (1967) who described the high similarity of the composition of droppings from bigger Diplopoda, Tipulidae and Lumbricidae of the genus *Dendrobaena*.

All anecic earthworm species are especially efficient in the *coarse mixing of organic and mineral material* near the mineral soil surface. These species can be replaced to a great extent, sometimes even totally, by *Lumbricus rubellus* which, as indicated above, is less susceptible to acids. This is even more so in cases where *L. rubellus* is supported by endogeic species. So Ehrmann (1991) found a deeply developed mull with an overground residence time of the litter of at most one year in an oak forest location without deep-burrowing earthworm species but with *L. rubellus*, *Aporrectodea caliginosa* and *A. rosea* (Saviny, 1826).

Scheu and Sprengel (1989) found in a laboratory experiment that *A. caliginosa* can mix beech leaf material with mineral soil if it has been comminuted before by the millipede *Glomeris marginata* (Villers), 1789. David (1987) gives a report from an oak forest location with humus form F-mull where anecic earthworms only occur in very low abundances. Here the coarse mixing apparently is the result of the combined activity of larger millipeds and endogeic earthworms. However, as the large macrophytophagous millipeds occurred in high abundances only on sites with a pH (H₂O) above 4.0, they will not be able to replace earthworms eliminated

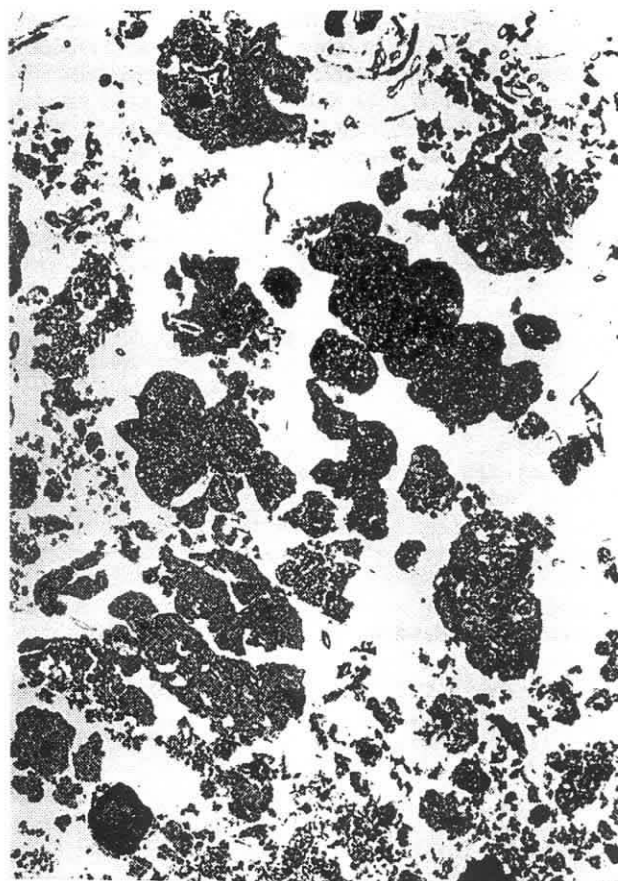


Figure 6. – Loose soil fabric of irregularly broken and often roughly rounded aggregates by burrowing activity of voles (all aggregates in the lower part), the smoothly rounded aggregates are earthworm casts (centre, left of centre, from centre to top right). – Young beech forest (natural regeneration), Ah-horizon, mull, Braunerde-Pseudogley (cambisol to stagnic gleysol), loess and Jurassic sandstone and clay. – Thin section, natural height 20 mm.

by acidification. – Finally, it must be remembered that in deciduous forests a mixing of plant residues into the mineral soil often is the result of the burrowing activity of voles (Babel, 1981).

To a great extent, there are examples of substitution for each other between different groups of soil animals in the *fine mixing of organic and mineral material*. In nearly all groups of saprophagous soil animals

there are species which ingest frequently mineral and organic materials together. Therefore, fine mixing is a good example for substitution ability.

Biological formation of aggregates and voids is another case of redundancy. As a rule, similar feeding activity leads to similar dropping aggregates. These may form similar dropping fabrics with specific interaggregate voids. This applies to F-, H- and Ah-horizons and, there, to different species of enchytraeids and microarthropods. At the surface of the mineral soil, in the Ah and in deeper horizons of the mineral soil, it applies to species of endogeic earthworms. Their channels and their infillings appear to be little species-specific; this means redundancy. – In the formation of aggregates and voids voles can also replace deep-burrowing earthworms (fig. 6). However, these animals apparently are dependent on thick layers of deciduous litter as they occur for example in natural regeneration stands of beech with litter accumulation by wind (Babel, 1981).

CONCLUSIONS

Redundancy is an important stabilizing principle of forest humus profiles. It was shown that for all of the four morphologically visible profile-forming processes, viz. comminution of plant residues, coarse mixing, fine mixing and biogenic fabric formation, there are examples of several co-occurring animal species with the ability to perform them. In comminution and fine mixing substitution is possible within a broad limit, because there are many coexisting species. In the other two processes, exerted mainly by earthworms, possibilities of species replacement are much more limited. The ability of substitution for earthworm species is restricted to animals with similar or greater strength and mobility. These are other earthworm species, possibly assisted by large millipeds, and voles.

As was shown above, two given species may occur together on one site and alone on others. More information on the mechanisms determining co-occurrence of species would enable us to make more precise and reliable assertions on extend and limits of redundancy in forest humus profiles.

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